

STUDIES IN GRINDELIA. III¹

JULIAN A. STEYERMARK

*Assistant Curator of the Herbarium, Field Museum of Natural History, Chicago
Formerly Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany
of Washington University*

HISTORY OF THE GENUS

In 1804 Sessé introduced seeds from Mexico to the Royal Gardens at Madrid where they were grown in 1805 under the name of *Aster spathulatus* Hort. Seeds from these plants were sent to the Montpellier Garden (Hortus Monspeliensis), and from plants grown there were distributed to various botanical gardens. Willdenow, of the Berlin Botanical Garden, received some from Professor Broussonet of Montpellier in the spring of 1806 under the name of *Aster spathularis*. When the plants flowered and matured fruit during the summer of 1807, Willdenow observed that they differed from *Inula*, under which Persoon² had identified them, and from *Aster* (the only genera known to him at the time with which his plants might have shown relation). Accordingly he described³ from them a new genus, *Grindelia*, in honor of Professor Grindel of Dorpat, and named the particular plant *Grindelia inuloides*.

Previously, in 1793, Cavanilles⁴ had described and illustrated an *Aster glutinosus* based upon plants he had seen in flower in the Royal Gardens at Madrid, and stated that they had come originally from Mexico. Although the ligules were yellow, a character at variance with *Aster* but in common with *Inula*, he decided that color alone should not serve as a criterion in distinguishing genera of Compositae. He regarded the nature of the base of the anther as of more fundamental impor-

¹ This, the third installment of studies in *Grindelia*, is a continuation of the monographic work which was carried on at the Henry Shaw School of Botany while the author was engaged in a comprehensive study of the genus.

² Persoon, C. H. Syn. Pl. 2: 451. 1807.

³ Willdenow, C. L. Ges. Nat. Fr. Berlin Mag. 1: 260. 1807.

⁴ Cavanilles, A. J. Ic. et Descr. Pl. Hisp. 2: 53. pl. 168. 1793.

tance. The fact that the anthers were entire at the base as in *Aster* rather than bisetose as in *Inula* led him to place the species under *Aster*.

Willdenow³ observed that Cavanilles⁴ had figured the ray florets of *Aster glutinosus* without pappus bristles, although he did not mention this point in his description. No species of *Aster* (except a few with pinnate leaves) were known at that time to possess yellow flowers, and this fact, together with the absence of pappus bristles on the ray flowers, led him to place the plant in the genus *Doronicum* and to publish it as *Doronicum glutinosum*.⁵ Between 1800 and 1807 seeds of *Aster glutinosus* had been grown in the various botanical gardens of Europe and Great Britain. During this time Willdenow had examined living plants and found that all the florets possessed pappus bristles. This led him to reconsider his identification, with the result that in 1807 he placed⁶ the plant with *Aster* as Cavanilles originally had done. Persoon,⁷ in his 'Synopsis Plantarum' in 1807, treated *Aster glutinosus* and *Grindelia inuloides* as congeneric with *Inula* and described them respectively as *Inula glutinosa* and *I. serrata*.

In 1813 Nuttall⁸ published without description a generic name, *Thuraria*, which proved later to be congeneric with *Grindelia*. Robert Brown,⁹ the same year, recognizing that *Doronicum glutinosum* (*Aster glutinosus*) had no relationship with either *Doronicum* or *Aster*, erected for it a new genus *Donia* which he based primarily on its caducous bristly pappus. This genus was adopted by Pursh,¹⁰ and a new species *Donia squarrosa*, from the Missouri River prairies, was described.

Lagasca¹¹ in 1816 was the first to recognize that the *Aster spathulatus* Hort. and the *Aster glutinosus* were congeneric and constituted a new genus *Demetria*, with two species *De-*

³ Willdenow, C. L. Sp. Pl. 6^a: 2115. 1800.

⁴ Willd. Ges. Nat. Fr. Berlin Mag. 1: 259. 1807.

⁵ Persoon, C. H. loc. cit. pp. 451-452. 1807.

⁶ Nuttall, T. in Fras. Cat. 1813.

⁷ Brown, Robert. in Ait. Hort. Kew, ed. 2. 5: 82. 1813.

⁸ Pursh, F. Fl. Am. Sept. 2: 559. 1814.

⁹ Lagasca, M. Gen. et Sp. Pl. Nov. 30. 1816.

metria spathulata and *D. glutinosa*. A year previous, Cassini¹² had proposed a new genus, *Aurelia*, for the *Aster glutinosus* of Cavanilles (*Inula glutinosa* Persoon) to be placed next to *Grindelia* taxonomically.

Some confusion as to the generic limits of these recently proposed genera (*Grindelia*, *Donia*, *Demetria*, and *Aurelia*) existed between 1815 and 1819. In 1815 Robert Brown, on comparing flowering material of *Grindelia inuloides*, grown in the Kew Gardens, with his *Donia glutinosa*, found that the two differed principally in the number of pappus awns to the floret—there being one or two in *Grindelia inuloides* and a greater and more indefinite number in *Donia glutinosa*. Realizing that this was a variable character in *Donia* and that the two species were otherwise essentially alike, he abandoned¹³ *Donia* and reunited it with *Grindelia*, since *Grindelia* was the genus first published. Dunal,¹⁴ in 1819, showed further that *Grindelia*, *Donia* and *Demetria* were entirely congeneric and should constitute one genus, *Grindelia*, that being the name first published and already generally recognized. Kunth was in agreement with this treatment.

Cassini¹⁵ tried to show that *Donia* and *Aurelia* were distinct from *Grindelia*, first, because in the former two genera the awns of the pappus were “barbellate,” whereas in *Grindelia* they were “unappendaged,” and second, the anthers in *Donia* and *Aurelia* did not have basal appendages, whereas *Grindelia* did. Although, according to Kunth, in the true *Grindelia* the anthers were naked at the base, Cassini stated that he had found “two basal semilanceolate or subulate appendages” on each anther. Again, in 1825, Cassini¹⁶ insisted on the validity of retaining *Aurelia* distinct from *Grindelia*, and reported a third difference, namely, that *Grindelia* had one to three, or occasionally more, pappus awns to the floret, whereas in *Aurelia* they were numerous; moreover, although he was aware that

¹² Cassini, H. Bull. Soc. Philom. p. 175. 1815.

¹³ Brown, Robert. Trans. Linn. Soc. London **12**: 102. 1818.

¹⁴ Dunal, F. Mem. Mus. Par. **5**: 46. 1819.

¹⁵ Cassini, H. Jour. Phys. **89**: 32. 1819.

¹⁶ Cassini, H. Diet. Sci. Nat. **37**: 468. 1825.

Aurelia was antedated by *Donia*, he felt that *Aurelia* should be retained since Robert Brown had not only abandoned *Donia* but also was unaware of its real distinctive characters. However, later studies have shown that both few and numerous awns were found, and only one type of anther, that with short, broad, deltoid bases. Rafinesque,¹⁷ in 1818, attempted to displace *Donia*, with the remarks: "*Donia* is rather too short, and contained in *Cladonia*, etc., it ought to be lengthened into *Doniana*." A year previous Cornelissen¹⁸ published a new genus, *Hoorebekia*, with one South American species, *H. chiloensis*. For some time this genus had been identified with *Aplopappus*, but recently has been shown¹⁹ to be a *Grindelia*, congeneric with and antedating the South American species, *Grindelia speciosa*, *G. resinosa*, *G. foliosa*, and *G. Volkensii*.

Dunal,²⁰ in 1819, described six species of *Grindelia*, of which *G. pulchella* and *G. angustifolia* (the latter belonging to another genus) were new, and *G. glutinosa*, *G. inuloides*, *G. squarrosa* and *G. fruticosa* had been transferred from other genera. In 1825 Cassini,²¹ still regarding his genus *Aurelia* as distinct from *Grindelia*, published two species, *A. amplexicaulis* and *A. decurrens*.

From 1825 on many species and varieties of *Grindelia* were published. In 1836 A. P. DeCandolle²² treated *Grindelia* in the 'Prodromus,' describing thirteen species of which seven were new; and in 1838²³ he added four more, one, *G. stricta*, being new. In 1841 Nuttall²⁴ described five new species of *Grindelia*, and in 1842 Torrey and Gray²⁵ recognized ten species in their 'Flora of North America.'

In 1857 a new genus, *Chrysophthalmum*, with one species, *C.*

¹⁷ Rafinesque, C. S. Am. Month. Mag. p. 268. 1818.

¹⁸ Cornelissen, E. N., in Mussche, J. H. Hort. Gand. p. 13. 1817.

¹⁹ Hall, H. M. Carnegie Inst. Wash. Publ. No. 389: 24. 1928.

²⁰ Dunal, F. loc. cit.

²¹ Cassini, H. loc. cit.

²² DeCandolle, A. P. Prodr. 5: 314. 1836.

²³ Ibid. 7: 278. 1838.

²⁴ Nuttall, T. Trans. Am. Phil. Soc. N. S. 7: 314. 1841.

²⁵ Torrey, J. and Gray, A. Fl. N. Am. 2: 246. 1842.

andinum, was described by Philippi²⁶ from the Andes of Chile, and seven years later he²⁷ transferred it to *Grindelia*. This species is also recognized by Cabrera under *Grindelia*, but, for the present at least, the writer prefers to regard it as generically distinct.

Gray,²⁸ in two editions of the 'Synoptical Flora of North America,' 1884 and 1888, recognized twelve species with several varieties, reducing a number of species to synonymy. Since 1888 approximately fifty-eight species, varieties, and forms of *Grindelia* have appeared in the literature bringing the total number of names described to nearly one hundred and forty.

GEOGRAPHICAL DISTRIBUTION

The environmental factors, past geological history, and the present distributional areas of the different species of *Grindelia* are very closely correlated. Many of the species have a remarkable capacity to pioneer and spread into new or previously unoccupied territory. Their aggressiveness is associated with their natural ability to thrive in open exposed or recently cleared or eroded habitats. They will often be the first or among the first plant forms to invade open places along roadsides, roadcuts, irrigation ditches, alluvial deposits of streams, recently eroded slopes, over-grazed pastures, railroad tracks, waste places, etc. Especially the prairie and plains species, notably *G. squarrosa*, *G. squarrosa* var. *serrulata*, and *G. perennis*, are among the most conspicuous examples of invaders, and are among the worst weeds, frequently being classed by agriculturists as obnoxious plants.

Associated with this weed tendency is the fact that the majority of the species form colonies. The reason is quite obvious when one considers the definite relation between colony-formation and the pappus of the genus. The few pappus bristles are awn-like and therefore not adapted for wind dispersal as in

²⁶ Philippi, R. A. *Linnaea* 29: 9. 1857.

²⁷ *Ibid.* 33: 137. 1864.

²⁸ Gray, A. *Syn. Fl. N. Am.* 1st: 116. 1884, and ed. 2. 1888.

many Astereae where the achenes have a light plumose pappus. When the achenes are ripe in *Grindelia*, the receptacle and involucre gradually open. The achenes, with the pappus mostly lacking, are much too heavy to be carried away by the wind, and when shaken out they fall to the ground close to the parent plant. Most of the seeds are viable and germinate readily. Numerous seedlings spring up around the parent plant forming compact mats by the thousands. Year by year the colony gradually increases, both in number of plants and in area. This colony formation is particularly well shown in *G. squarrosa* and var. *serrulata*, *G. perennis*, *G. lanceolata*, *G. nana*, *G. decumbens*, and *G. camporum*.

The majority of the species are found growing in strongly alkaline or saline to circumneutral soils. The apparent preference for strongly saline soils is well shown in *G. humilis*, *G. Blakei*, *G. stricta* and varieties (excluding var. *collina* and var. *Hendersoni*), and *G. aggregata*, which occur in salt or brackish marshes, tidal estuaries, and marine sand beaches. *Grindelia perennis* and *G. camporum* are often found about saline flats, salt lakes and springs, and alluvial rich soils of alkaline streams. *Grindelia texana* is mostly confined to limestone glades of the Edwards Plateau in Texas, and *G. lanceolata* to limestone and dolomite areas in Tennessee, Alabama, Missouri, Arkansas, and to a limited extent in Oklahoma and Texas. In Missouri *G. lanceolata* is limited in the Ozark region to limestone and dolomite glades of the Jefferson City (Beekmantown) and Joachim formations of Ordovician age and to the Mississippian limestones of the extreme southwest. Its absence over most of the central and southeastern Ozark region is due to the fact that either acidic rocks of Roubidoux sandstone cap the surface or the surface is underlain mostly with granite, chert, or sandstone. Similarly, *G. grandiflora* is limited in the United States to the limestone of the Devil's River and adjacent Texas region. Sometimes the soils occupied are clayey and rich in nutritive elements, rather than rocky limestone. For example, *G. camporum* var. *Davyi*, *G. procera*, *G. aphanactis*, and *G. squarrosa* follow the alluvial

silts and clays of river banks, and may spread out into adjacent fields or prairies. A number of species occur in the immediate vicinity of the ocean, as *G. arenicola*, *G. rubricaulis* and its varieties *robusta*, *elata*, and *latifolia*, and *G. stricta* var. *collina* and var. *Hendersoni*. According to Cabrera,²⁹ the South American species tend somewhat to grow in alkaline soils.

Practically the whole range of the species of *Grindelia* may be included in the Lower and Upper Sonoran of the Austral zone and the Arid and Humid transition zones. This relatively small zonal range is remarkably correlated with the present areas occupied and the major climatic environmental factors of rainfall, temperature, and altitude.

The species are unusually adapted to xerophytic, semi-desert, or desert environments, sometimes occurring in regions which receive annually ten inches or less of rainfall. Such habitats are wind-swept plains and prairies, limestone glades, dry rocky plateaus and mesas, sands and dunes along the rivers and seashore, exposed clayey and rocky slopes, dry bluffs along river courses, etc., also salt marshes and tidal estuaries which are physiologically quite dry.

Some species have a remarkable capacity of germinating in very moist or inundated soils, and later, as the particular areas gradually become desiccated, are able to adapt themselves to the new conditions. *Grindelia squarrosa* var. *nuda* and var. *nuda* f. *angustior*, for instance, in Texas, are frequently confined to lake-beds which fill with water in times of heavy rainfall but for years at a time may remain dry and become extremely xerophytic. Also, *Grindelia procera* germinates along the San Joaquin River Valley in spring and early summer in inundated places which later become very dry and parched. The same adaptations may often be observed in the Californian *G. camporum* and *G. camporum* var. *Davyi*.

In view of the above statements, it is not surprising that *Grindelia* is more or less generally distributed over western North America. In the United States the genus has been re-

²⁹ Cabrera, A. L. Revision de las especies Sudamericanas del genero "*Grindelia*." in Rev. Mus. La Plata 33: 208. 1931, and in letter.

corded from every state except Kentucky, Mississippi, Florida, South and North Carolina, and West Virginia. It is commonly introduced east of Illinois and reaches all the New England States. North of the United States the genus penetrates to

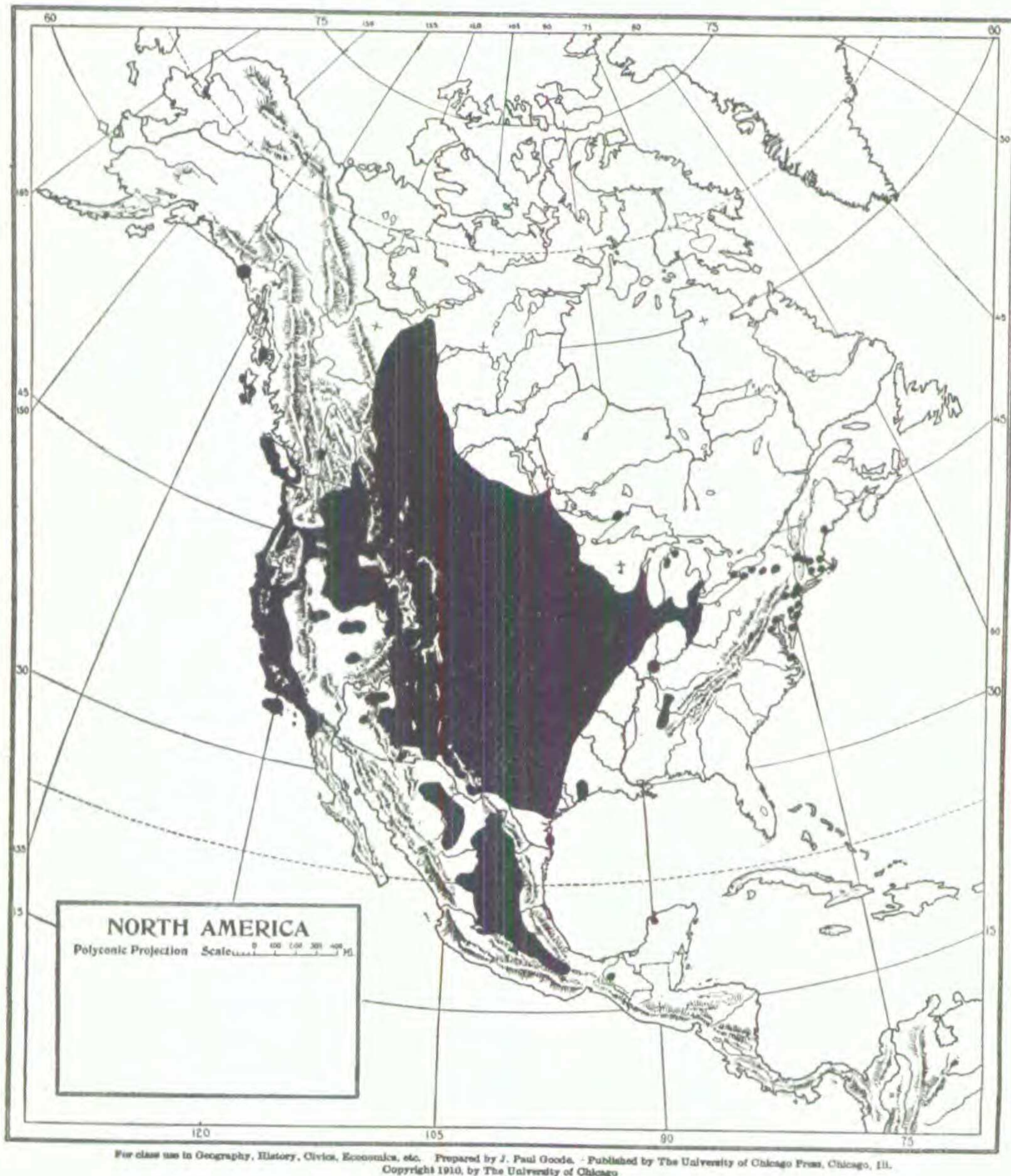


Fig. 1. Distribution of the genus *Grindelia* in North America.

59° 34' North latitude about Port Mulgrave, Alaska, and slightly north of 60° North latitude in the vicinity of the Great Slave Lake region (Wood Buffalo Park and salt plains about Bear Spring, etc.) in Northwest Territory. It is naturally distributed in the United States west of the 86th Meridian (fig. 1).

It occurs in Mexico over the greater portion of the Plateau, but no collections have as yet been seen from the state of Sonora. One species, *G. perennis*, has been introduced in Yucatan. So far as records occur the genus skips Central America, and then reappears in South America, in Peru, Uruguay, Paraguay, southern Brazil, and in Argentina south to the Santa Cruz region. Altitudinally it ranges from sea-level to approximately 10,000 feet in the mountains of the state of Hidalgo, Mexico. The genus is predominantly one of open places and is practically absent from deep forests or wooded areas. The few species or varieties that do penetrate wooded areas are found in rather thin and semi-open tracts or near the borders of woods.

Many of the species of *Grindelia* occur on geologically very youthful territory, in most cases of Pleistocene or Post-Pleistocene age. Areas from which the sea has withdrawn or where emergence has followed submergence, places of recent sedimentation or vulcanism, glaciated areas from which recent ice-sheets have retreated, recently eroded regions, and similar youthful places have been quickly populated by species of *Grindelia*, especially if such places offered open habitats in Sonoran or Transition zones. Many of these species show rather restricted distributions which are the result of the past geological history. Notable examples are *Grindelia humilis*, which is not known outside of San Francisco and Tomales Bays of California, *G. littoralis* restricted to the Galveston Bay region, and *G. oolepis*, around Brownsville, Texas. Other coastal endemics, *G. Blakei* and *G. aggregata*, show themselves to be of at least Pleistocene or Post-Pleistocene dispersal, since the particular coastal areas occupied have all been submerged by sea water during Quaternary times and some even into the Recent epoch. The recent subsidence, which permitted the sea to encroach upon the river valleys, forming the Bay of San Francisco and other bays along the coast took place practically in modern times. Similarly, the deposits along the outermost margin of the Gulf and Atlantic Coastal Plain, including the Gulf Coastal strip of Texas, are mostly of

Recent or Quaternary origin; the bays and coastal region about Brownsville and Galveston have had the sea withdrawn from them only a matter of thousands of years.

In contrast to the coastal species of very limited distribution are those coastal types which are rather widely distributed along the Pacific Ocean and also occur on land of Recent or Quaternary origin. The extensive fiords and inlets along the coast of Alaska and British Columbia represent drowned river valleys of Recent and Quaternary submergence. Vancouver Island and the Queen Charlotte and adjacent islands are the projecting spurs of a range paralleling and even more submerged than the coast range to the East. About the close of the Pliocene there was elevation of the entire west coast³⁰ which continued into early Pleistocene, but toward the middle of Pleistocene the entire coast range area was sunk 1000 to 2000 feet.

Following the glacial epoch another period of subsidence occurred in the Lower and Upper San Pedro epoch, during which the shore line was carried downwards 300 to 700 feet lower than at present, drowning the mouths of streams and erosion valleys entering the ocean. Then occurred an elevation which was soon followed by another submergence, resulting in the present shore lines of Oregon and California. The northern two-thirds of the coast region in Oregon consists mostly of Miocene sandstone and shales, and the bold cliffs and promontories comprise mostly Tertiary basalt; the southern third is made up mainly of Quaternary gravel, sand, and silt.³¹ In the southern coast region of Oregon the surface sands along various portions of the coast are of Pleistocene age.³² Evidence that the coast of Oregon and Washington has recently emerged is to be seen in the narrow coastal plain one to twenty miles wide. Even more

³⁰ For discussion of geologic and physiographic history, see Fenneman, N. M. *Physiography of western United States*. pp. 479-506. 1931; Jepson, W. L. *Manual of flowering plants of California*. pp. 10-11. 1925; Smith, J. P. *Salient events in the geologic history of California*. *Science N. S.* 30: 346-351. 1909.

³¹ Peck, M. E. *A preliminary sketch of the plant regions of Oregon*. I. *Western Oregon*. *Am. Jour. Bot.* 12: 36. 1925.

³² Peck, *loc. cit.* pp. 45-46.

recent is a subsidence which has drowned the streams across this coastal plain and extending far inland. The Chehalis River has been drowned for 30 miles, the Columbia 140 miles, the Umpqua 25 miles, and the Coquille 30 miles.³³

The entire coast strip of California is composed of sands, gravels, or muds, of Recent or Quaternary origin. Puget Sound constitutes the northernmost portion of a huge trough of crustal deformation; this trough includes the Great Valley of California, probably the Gulf of California, the Willamette Valley of Oregon, the Cowlitz, upper Chehalis and Puget Sound Valleys of Washington, and to the northward the sounds separating Vancouver and the Queen Charlotte Islands from the mainland of British Columbia.³⁴ Puget Sound was extensively glaciated in the Pleistocene, and, after the disappearance of the ice sheet, was depressed, thereby allowing the sea to advance and drown the mouths of rivers. The Puget Trough has sunk and been submerged several times since post-Cretaceous, during much of Tertiary time having been a sinking geosyncline.³⁵ The present deposits and topography of this region are the results chiefly of erosion in the interglacial and last glacial epochs.³⁶

Since the present coastal strips of Alaska, British Columbia, Vancouver Island, Queen Charlotte and adjacent Islands, Puget Sound, Washington, Oregon, and California are all of Recent or Quaternary origin, the species of *Grindelia* occurring on these coastal strips must likewise be very recent. Also, it is in keeping with their pioneering tendencies that they should have invaded this coastal strip. Nor is it surprising that many of these species should be so very variable. The variations have not as yet had sufficient time to differentiate into distinct entities, but form an interwoven complex. For example, *G. rubricaulis*, with its numerous varieties and forms, ranges along the coast from northernmost Lower California to northern Marin County, California, assuming many variations in its extent northward: var. *latifolia*, occurring on the

³³ Fenneman, *loc. cit.* p. 461.

³⁵ Fenneman, *loc. cit.* p. 450.

³⁴ Fenneman, *loc. cit.* pp. 442-443.

³⁶ Fenneman, *loc. cit.* p. 451.

Santa Barbara Islands and on the adjacent mainland, which gives rise to several forms on the mainland; var. *platyphylla* around the Monterey Bay region; and var. *robusta* along the coast from Orange to Santa Cruz County. From the dunes in the region of Carmel, Monterey County, California, and ranging north along the coast to Coos County, Oregon, is the coastal species, *G. arenicola*, which is generally found on the most recent coastal dunes, mesas and beaches.

Grindelia stricta, with its varieties, is another of the rather wide-ranging coastal types, being distributed from southern Alaska in the vicinity of Port Mulgrave south to Mendocino County in northern California. It is a more or less distinct species throughout this range, but in the Puget Sound region and in the Sound to the north between Vancouver Island and the mainland of British Columbia, it gives rise to series of extremely perplexing variations. A robust form with large leaves and heads, var. *macrophylla*, occurs along the larger estuaries farthest removed from the direct ocean currents; another variation, var. *lanata*, with more or less pronounced pubescence on stem, leaves, and involucre, is found along the seashore often on rocky shores; var. *aestuarina*, with more sharply serrate, firmer, more resinous leaves and more resinous involucre, is very common in the salt marshes, estuaries, and sand beaches in the Puget Sound region; var. *Andersonii* in salt marshes around Saanich Arm, southeastern Vancouver Island, has become exceedingly foliose towards the heads; and var. *collina*, another variation of the same series, has betaken itself to dry terrestrial habitats where it has developed smaller heads and slender resinous leaves. It is interesting that the range of *G. stricta*, including all its varieties and forms, is approximately that of *Glehnia leiocarpa* Mathias,³⁷ but *Glehnia leiocarpa* has not differentiated into a number of variations as has *G. stricta*. The localization to certain estuaries of varieties of *Grindelia*, especially those on the Pacific Coast, is somewhat analogous to the estuarine problems of variation,

³⁷ Mathias, M. Studies in the Umbelliferae. I. Ann. Mo. Bot. Gard. 15: 95-101. 1928.

isolation, and endemism in the genus *Bidens* in eastern North America.³⁸

A very striking correlation exists between the present distributions of certain species of *Grindelia* and the recent geological history of the Willamette Valley, the Puget Sound, and Puget Trough regions. According to Fenneman, the Puget Trough is "a long valley enclosed on the east by the cascades and on the west by the Olympic Mountains and the Oregon Coast Range. Its northern end (within the United States) is occupied by Puget Sound. Its southern end is the Willamette Valley in Oregon."³⁹ While the Puget Trough was a sinking geosyncline it was receiving sediments. It was then uplifted, and the erosion which followed resulted in Willamette and Sound valleys. "These newer lowlands have since been in large part buried; in the north by glacial drift and outwash; in the south by sediments deposited when the Willamette and lower Columbia Valleys stood for some time below sea-level."⁴⁰ During the melting of the last ice sheet the Willamette Valley lay below sea-level. "The valley of the Columbia, both east and west of the Puget Trough was a strait. This was at the time when Puget Sound was last depressed, following the disappearance of the ice sheet. Over most of the Willamette Basin the soil is derived from sediments laid down in this sound."⁴¹ In late Pleistocene the sea advanced up the Columbia River and flooded the present Willamette Valley.⁴² Also during the course of the last Puget Sound submergence the higher mountain ridges were left standing as projecting islands (San Juan and others).

³⁸ For discussion, see Fernald, M. L. Some noteworthy varieties of *Bidens*. *Rhodora* 15: 74-78. 1913; Fernald, M. L. and H. St. John. Some anomalous species and varieties of *Bidens* in eastern North America. *Rhodora* 17: 20-25. 1915; Fassett, N. C. The vegetation of the estuaries of northeastern North America. *Proc. Bost. Soc. Nat. Hist.* 39: 76-118. 1928.

³⁹ Fenneman, *loc. cit.* p. 443.

⁴⁰ Fenneman, *loc. cit.* p. 451.

⁴¹ Fenneman, *loc. cit.* pp. 453-454.

⁴² Fenneman, *loc. cit.* p. 263; and Bretz, J. H. The late pleistocene submergence in the Columbia Valley. *Jour. Geol.* 27: 489-506. 1919.

Grindelia integrifolia and var. *virgata* occur only on the Quaternary gravels, sands, or silts of the Willamette Valley region north to Vancouver, Washington, and east to Hood River, Oregon (except for an isolated station of var. *virgata* on the San Juan Islands), whereas *G. stricta* var. *collina* and var. *lanata* have taken to the coastal rocky bluffs, seashore, and islands in and about the Puget Sound and the southern tip of Vancouver Island. After the flooding of the Pacific Coast, including Puget Sound and various subsidences, *G. stricta* became widely distributed in salt marshes, estuaries, sand beaches, and other coastal habitats from southern Alaska to northern California, giving rise to many variations in the Puget Sound area, *G. stricta* var. *lanata* and *G. stricta* var. *collina* being two. Upon the submergence by the Columbia of the Willamette Valley in late Pleistocene, the maritime *G. stricta* var. *lanata* intruded along the marginal beaches and shores of the Valley; then, upon the withdrawal of the sea and the later burial of the Willamette Valley by depositions of sand, gravel, and silt, its Puget Sound prototype which had penetrated this area was forced to take to the dry land of the Willamette Valley region where it has given rise to *G. integrifolia*. When the San Juan, Vancouver, and other islands were left standing in Puget Sound, *G. stricta* var. *collina* became the terrestrial phase of *G. stricta*; and at the time the Willamette Valley was depressed along with the rest of the Puget Sound, the maritime types invaded the Valley. Then, following the withdrawal of sea water and the consequent deposition, the maritime types took to the dry lands; but *G. stricta* var. *collina*, following this connection between the submergence of the Puget Sound and Willamette Valley, gave rise in the Willamette Valley region to *G. integrifolia* var. *virgata*. As a relic pointing to the former submergence of these portions of the Puget Trough we find this variety (outside of its occurrence in the Willamette Valley region) isolated on one of the projecting portions of the San Juan Islands. The Willamette Valley region, its floor covered by Quaternary and Recent deposits, has a fair number of species restricted to it. These

endemics are practically all species just beginning, excellent examples of which are *Sidalcea campestris* and *S. virgata*.⁴³

Grindelia camporum and its varieties are found in the Great Valley of California and southwestern Oregon, that is, the San Joaquin and Sacramento River valleys, the Tulare Basin, the western lower foothills of the Sierra Nevadas and the foothills of the northern and central Coast Range, and the river valleys of southwestern Oregon. Practically all of the floor of the Great Valley is covered with Pliocene, Pleistocene, or Recent alluvium, consisting of clay, sand, or gravel, most of it being of Recent or Quaternary origin. Several times during the Eocene and Pliocene and in the Pleistocene it was an inland sea.⁴⁴ Its successive sinking, often followed by seaward invasion, has been linked with the history of the surrounding Coast and the Sierra Nevada Ranges which have been continually warped upward. In the Lower and Upper San Pedro Epochs (Champlainian) of Quaternary time, when the surrounding ranges were much uplifted, much of the unconsolidated filling of the basin has accumulated. Even more recently (Terrace Epoch of Quaternary time) terraces were formed in the fluvial sediments in nearly all the Coast Range Valleys.⁴⁵ Obviously, *G. camporum* and varieties, as well as many other species of the Great Valley, must have migrated into it since Quaternary or even Recent times.

Grindelia nana and its varieties and forms, most closely allied to *G. camporum* var. *Davyi*, occupy the youthful territory of the Columbia Plateau (Oregon, Washington, Idaho) and adjacent regions in northern Nevada, California, and western Montana. Most of the rocks of the Columbia Plateau are the result of great outpourings of lava of Tertiary (beginning

⁴³ Roush, E. M. P. A monograph of the genus *Sidalcea*. Ann. Mo. Bot. Gard. 18: 175-179. 1931. See also Peck, M. E. Am. Jour. Bot. 12: 39-41. 1925.

⁴⁴ Jepson, W. L. Manual of flowering plants of California. p. 10. 1925; and Anderson, W. C. Proc. Cal. Acad. Sci. IV. 3: 6, 7, 32. 1908.

⁴⁵ For discussion, see Smith, J. P. *loc. cit.*; Fenneman, N. M. *loc. cit.* pp. 472-481, especially *fig. 165.* with bibliography; Bryan, K. Geology and ground-water resources of the Sacramento Valley, California. U. S. Geol. Survey, Water Supply Paper No. 495. 1923.

with the Miocene) and Quaternary times. The Snake River Plain has been covered with great quantities of Pleistocene basalt. The lavas throughout the range of *G. nana* and varieties are generally alkaline. Most of the valleys of the mountain region of Idaho where the species occurs are covered with Quaternary deposits.⁴⁶ Many of the valleys of western Montana are filled with Tertiary and later sediments. "The upper Flathead Valley is . . . underlain in part by Miocene beds and partly filled by glacial deposits."⁴⁷

The distribution of *G. columbiana* is definitely correlated with the late Pleistocene submergence of the area occupied. This species is practically restricted to the immediate environs of the Columbia River and some of its branches (Yakima River) in Washington and Oregon and to a limited extent the Snake River in Idaho. The Columbia River in this region flows through the Tertiary and Quaternary lava deposits. The last cycle of erosion of the cuttings of the Columbia River gorge is also Recent. Coulees are associated with the Pleistocene drainage of this river. "They represent approximately the normal drainage lines of the present-day but more accurately the lines of Pleistocene drainage. . . . These coulees and scablands result from erosion by glacial streams of great volume and steep gradient escaping from the ice-covered area to the north."⁴⁸ They are the abandoned courses of ancient rivers extending in Washington from the Snake River north to the Spokane and Columbia Rivers, and west to the Columbia River (including Douglas, Lincoln, Adams, and part of Yakima and Franklin Counties). The largest of the coulees are Grand Coulee and Moses Coulee. During the Wisconsin glacial epoch of Pleistocene time a glacial lobe of the ice sheet from the Okanogan Valley west of the Grand Coulee covered the Columbia River, crossing and blocking the Columbia Gorge, and damming back the waters until they rose to the level of the former Grand Coulee. This caused the waters to find a temporary new channel through the Grand Coulee. Following the depression in

⁴⁶ Fenneman, *loc. cit.* pp. 185-196.

⁴⁸ Fenneman, *loc. cit.* pp. 258-259.

⁴⁷ Fenneman, *loc. cit.* p. 208.

the Grand Coulee to the lower course of Crab Creek the waters of the Columbia River finally rejoined the main course of the river.⁴⁹ After the withdrawal of the glacial lobe and retreat and melting of the ice, the Columbia again followed its present course, leaving the Coulees as abandoned water courses. In late Pleistocene time the Columbia River was flooded by marine waters which submerged Yakima and Walla Walla Valleys.⁵⁰ The occurrence of *G. columbiana* at Grand Coulee above Blue Lake, Grant County, and at Wilson Creek, Whitman County, shows that it had followed the course of the Columbia River when the waters were forced to flow temporarily through the channels of the Coulees.

The distributional ranges of various species of *Grindelia* are closely correlated with the several floristic provinces maintained by Peck⁵¹ in his preliminary study of plant regions of Oregon. These natural plant regions are the Northern Coast Region, Northern Coast Mountain Region, Willamette Valley Region, Rogue-Umpqua Region, Southern Coast Region, Southern Coast Mountain and Siskiyou Region, Cascade Region, Eastern Oregon Region (subdivided into the Columbia River Area, Yellow Pine Area, Bunch-grass Area, Lake Area, and Sagebrush Area), and the Blue Mountain Region.

The restriction of *G. integrifolia* and *G. integrifolia* var. *virgata* to the Willamette Valley region has already been discussed. Placing the Columbia River area under the Eastern Oregon Region takes care of the confinement of *G. columbiana*. The separation of the coastal flora into the Northern and Southern Coast Regions at approximately the mouth of the Coquille River is also a very natural division. At this point there is a strong break and contrast in floras, that to the south being decidedly Californian, whereas that to the north is the northern coastal flora which ranges from Alaska or British Columbia southward and sometimes penetrates into Califor-

⁴⁹ Fenneman, *loc. cit.* pp. 256-263.

⁵⁰ Bretz, J. H. The late pleistocene submergence in the Columbia Valley. *Jour. Geol.* 27: 489-506. 1919; see also Fenneman, *loc. cit.* p. 263.

⁵¹ Peck, M. E. A preliminary sketch of the plant regions of Oregon. I. *Am. Jour. Bot.* 12: 33-49; II. 69-81. 1925.

nia. Applying these coastal divisions to *Grindelia* we find that *G. arenicola* with its varieties is mostly Californian, but reaches Oregon at the mouth of the Coquille River (at the sand dunes at Bandon), the division point between northern and southern floras; north of Bandon along the Oregon Coast the only coastal species encountered is *G. stricta* which is the common coastal *Grindelia* from southern Alaska south to Mendocino County, California.

Grindelia nana, with variations, is mostly confined in Oregon to the Bunch-grass Area and part of the Lake Area of the Eastern Oregon Region, although it penetrates also into the Rogue-Umpqua and Southern Coast Mountain and Siskiyou Regions. It is absent from the Willamette Valley Region (where *G. integrifolia* and var. *virgata* occur) which is more humid and which has had recent connections with the ocean water. *Grindelia nana* is most closely allied morphologically to *G. camporum*, the connection being most obvious between *G. nana* var. *altissima* and *G. camporum* var. *Davyi*. The former is found in northern California in the vicinity of the Coast and Sierra Nevada Ranges and southwestern Oregon, whereas the latter is mostly in cismontane California from approximately middle California northward, often occurring in the foothills of the Coast Ranges and the western foothills of the Sierra Nevada.

Grindelia nana, with its varieties, is dispersed mostly in the Arid Transition and Upper Sonoran zones of Oregon, Washington, Idaho, northern California, northern Nevada, and western Montana, but its relationships are with the Californian *G. camporum* complex. This Californian element in the flora of Oregon and Washington is remarkably important. Piper⁵² points out that Upper Sonoran plants of the Columbian Basin have originated in part from California and in part from the Great Basin. Furthermore, the natural route of the California plants, as influenced in large part by the prevailing southwesterly winds, would be in northeastern California through the Klamath Gap made by the Klamath River and lakes. He

⁵² Piper, C. V. Contr. U. S. Nat. Herb. [Fl. Wash.] 11: 38. 1906.

also states that few of these Upper Sonoran plants have reached the Columbia Basin by way of the Willamette Valley and the Columbia River because the Rogue River Mountains of southwestern Oregon form a natural barrier. Similarly, most of the Californian element in the Humid and Arid Transition areas in Washington reached the Columbia Basin by way of the Klamath Gap.⁵³ These statements accord nicely with the relationship between *G. nana* and *G. camporum*. The latter, of Californian origin, has undoubtedly given rise through *G. camporum* var. *Davyi* to *G. nana* by way of *G. nana* var. *altissima*. The migration of *G. nana* and varieties from California northeastward to western Montana, Idaho, eastern Washington, and Oregon east of the Cascades has certainly taken place through the Klamath Gap. The natural barrier of the Rogue River Mountains and the Calapooia Divide has been effective against the northward migration of *G. nana* and var. *altissima* from southwestern Oregon into the Willamette Valley Region.

Grindelia squarrosa and *G. perennis*, the former of the central prairies, the latter of the high northern plains, generally occur on Tertiary or even more recent territory. Many glacial lakes were formed in the high plains of Canada in Alberta and Saskatchewan from Great Slave Lake southward into northern Montana when the region was covered and severely scoured by the great Keewatin ice-sheets of Pleistocene time. *Grindelia perennis* is found around such lakes on the plains at Calgary and Edmonton—a region not available for plant occupation until Post-Pleistocene times. Most of the remaining portion of the prairies and plains occupied by *G. perennis* and *G. squarrosa* is of similarly youthful soils, made up of glacial till or of Tertiary or Quaternary deposits.

Although the majority of the species of *Grindelia* are of Pleistocene or Post-Pleistocene dispersal, a few species occur in areas which are geologically older and which have been exposed and available for plant occupation since the end of the Paleozoic area. Such are the Ozark Plateau of Missouri, Arkansas, and eastern Oklahoma, the Edwards Plateau of Texas

⁵³ Piper, *loc. cit.* p. 43.

and the great Mexican Plateau. The Cretaceous seas failed to invade the Appalachian Upland or the Ozark Plateau or the Mexican Plateau. Then, at the close of the Cretaceous they were affected by a general uplift, and again, towards the close of the Tertiary period, the Appalachian Upland and Ozark Plateau were uplifted.⁵⁴ The Mexican Plateau has not been available for plant occupation since the close of the Paleozoic, but it has been free from sea invasions since Cretaceous times.⁵⁵

Fernald has found that the plants of the most ancient dispersal occupy the land areas which have stood above sea-level since Cretaceous or in some cases since the close of the Paleozoic (although in many instances plants which now occupy the most youthful territory, that is, the Atlantic Coastal plain, were originally those of the peneplained Appalachian Upland which were compelled by invasions of mesophytic plants, following uplifts and erosion, to move out onto this new area). He finds that those groups in eastern North America which are related to similar groups in the most ancient parts of the World (mostly in Australia, New Zealand, and South Africa, also to a more limited extent in the Falkland Islands, India, Malay Archipelago, western South America, and a few other places) today are persisting on these ancient Mexican uplands, uplifted Appalachians, and a few on the Ozark Plateau.

A number of species of *Grindelia* are limited in distribution to the Ozark and Mexican Plateaus and Appalachian Upland which have (in the case of the Ozark and Appalachian areas) been available for occupation at least since the close of the Paleozoic and, in the case of the Mexican Plateau, late Cretaceous. The Edwards Plateau of Texas has been more or less available since the beginning of the Cenozoic after the withdrawal of the Cretaceous seas. This does not imply necessarily that plants have occupied these old emergent conti-

⁵⁴ Fernald, M. L. Specific segregations and identities in some floras of eastern North America and the Old World. *Rhodora* **33**: 25-63. 1931.

⁵⁵ Schuchert, C. A. Textbook of geology. Part II. Historical geology. *pl.* 41, 42, and 45. 1924.

mental areas since late Cretaceous or late Paleozoic times, but that they are limited to such areas and consequently are older than those species which occur on areas generally not available until late Tertiary, Pleistocene, or even Post-Pleistocene times.

Grindelia lanceolata is confined to the southern Appalachian and Ozark Uplift region, on limestone glades and limestone prairies from central Tennessee and northern and central Alabama to the Ozark region of Missouri, Arkansas, southeastern Kansas, and eastern Oklahoma, penetrating slightly into northeastern Texas on upper Cretaceous limestone soils (*Drummond* from "San Felipe de Austin," in Gray Herbarium is of this species, but the locality may have been confused as this species has not been collected there since). Aside from the Texas collections, *G. lanceolata* lies entirely within the Southern Appalachian-Ozarkian Plateau, a region available for plant occupation since the close of the Paleozoic. It is more likely, however, that the species occupied this area about early Eocene time following the late Cretaceous uplift; nor is it unlikely that it arrived towards the close of the Tertiary period when the region was again uplifted.

Grindelia texana, which has either been derived from or given rise to *G. lanceolata*, is confined to Cretaceous strata of the Edwards Plateau and Texas Hills section of Texas⁵⁶ and the Arbuckle Mountain region of south-central Oklahoma. This area has not been submerged by the seas since the close of the Cretaceous period, and has been available for plant invasion since that time. It is very likely that *G. texana* entered there in early Eocene times or perhaps later. *Grindelia grandiflora*, confined to northeastern Mexico and the Devils River country of the Edwards Plateau in Texas, probably entered Texas at about the same time.

It is probable that the inter-migration of Mexican and South American species of *Grindelia* occurred no earlier than the close of the Cretaceous but more likely in Eocene or Miocene times, after which the Mexican and South American species

⁵⁶ Deussen, A. Geology of coastal plain of Texas west of Brazos River. U. S. Geol. Surv. Prof. Paper No. 126:3. fig. 2. 1924.

became separated and have diverged along their respective evolutionary lines.

As already stated, the oldest species of *Grindelia* occupying the oldest land areas are *G. lanceolata*, *G. texana*, and all the species of the Mexican Plateau. To this list might be added *G. scabra* and var. *neomexicana*, *G. arizonica* and varieties, *G. Havardii*, *G. grandiflora*, and perhaps several others. The youthful species have been derived from those occupying the Mexican, Ozark, and Edwards Plateau and Texas Hills region, or from species derived from occupants of the geologically more ancient areas. Many of these species, such as *G. oolepis*, *G. Blakei*, *G. humilis*, *G. littoralis*, etc. are endemics, just beginning their evolution. Some youthful species on young territory have a wide distribution, such as *G. perennis*, *G. stricta* and varieties, *G. squarrosa*, *G. rubricaulis* and varieties, and *G. nana* and varieties.

The fact that youthful species of approximately the same age and on comparatively equally youthful soils may have very broad or very limited ranges argues strongly against the age-and-area hypothesis. Additional evidence against it is the distribution of most of the species of the genus. The genus as a whole is a large one, consisting of 57 species, over 40 varieties (many of which are incipient species), and about 24 forms. It occupies a greater part of western North America and much of South America. However, its distribution is not due to its long period of evolution, but rather to its aggressive and pioneering tendency. Most of the species are exceedingly plastic because of their youth, and the many variations have not yet had time to differentiate themselves, nor have the geographic barriers been great enough to have accomplished this. The genus is to be compared very consistently with such youthful genera as *Aplopappus*, *Solidago*, and *Artemisia*. In the words of Fernald:⁵⁷

“Is it not singular that *Eriogonum*, *Crataegus*, *Rubus* & *Eubatus*, *Lupinus*, *Astragalus*, *Oenothera*, *Gilia*, *Phacelia*, *Pentstemon*, *Solidago*, *Aplopappus*, and *Artemisia* should have not even a single species associated with

⁵⁷ Fernald, M. L. Isolation and endemism in northeastern America and their relation to the age-and-area hypothesis. *Am. Jour. Bot.* 11: 568, 570. 1924.

the ancient types which inhabit Australia and New Zealand, and that only 0.02 of the total species of *Potentilla*, *Euphorbia*, *Aster*, and *Erigeron* should have reached those lands? Is it not equally noteworthy that, with the exception of *Crataegus* and the blackberries (*Rubus* § *Eubatus*), all the largest genera of the temperate North American flora should be centralized upon the Tertiary sea bottoms (relatively youthful country) of the Mediterranean and Austro-Russian basins of the Old World and in the vast area of youthful country west and southwest of the Mississippi? The blackberries are most virulent in central and western Europe, a region available to plants only since the Pleistocene glaciation, but likewise in the glaciated region and the Tertiary coastal plain of eastern North America. *Crataegus* has its phenomenal development in the eastern United States and southern Canada, where it must have produced a multitude of its species in post-glacial time.

“It should be perfectly obvious that these genera and likewise such overwhelmingly large genera of Europe and southwestern Asia (but not of Australia and New Zealand) as *Dianthus* . . . , *Silene* . . . , *Verbascum* . . . , *Cousinia* . . . , *Centaurea* . . . , and *Hieracium* . . . , are really very young, or if geologically old (*Crataegus* and *Rubus* for example), they have been encouraged by modern conditions to rapid multiplication. And, if we estimate success of plants by their ability to cover country, to take care of themselves, and to multiply their variations to the bewilderment of the best systematists, then these are surely successful genera.”

In the same article, speaking of the woody Veronicas of New Zealand and the genus *Hebe*, Fernald⁵⁸ points out that there is a “similar multiplication of modern species and varieties in many old genera of the northern hemisphere: *Salix*, *Carya*, *Betula*, *Quercus*, *Crataegus*, *Rubus*, *Tilia*, *Rhododendron*, and others, which date chiefly from Cretaceous time. It simply means that under favorable conditions ancient generic stocks may enter a cycle of rapid multiplication of species.”

RELATIONSHIPS OF THE GENUS

Following Bentham and Hooker,⁵⁹ Engler and Prantl,⁶⁰ and Gray,⁶¹ all authors have placed the genus *Grindelia* in the tribe Asteroideae or Astereae-Solidagininae. Formerly, however, there was not such a universality of opinion. Although many early authors included *Grindelia* with the Astereae, some placed

⁵⁸ Fernald, *loc. cit.* p. 571.

⁵⁹ Bentham, G. and Hooker, J. D. *Gen. Pl.* 2: 250. 1873.

⁶⁰ Engler, A. und Prantl, K. *Die Nat. Pflanzenfam.* IV⁵: 148. 1889.

⁶¹ Gray, A. *Syn. Fl. N. Am.* 1²: 116. 1884, and ed. 2. 1888.

it under Achyrideae, Chrysocomeae, or Solidagineae of the Astereae; others, like Cassini,⁶² combined *Grindelia*, *Aurelia* and *Xanthocoma* into the Grindeliaceae as a subdivision under the Solidagineae. Some followed Reichenbach⁶³ who proposed the name Grindeliaceae as a section of the Solidagineae,⁶⁴ to which were referred *Xanthocoma*, *Grindelia*, and *Donia*.

While the consensus of opinion is that *Grindelia* has been correctly placed in the tribe Astereae, the present writer has concluded that its affinity is with the tribe Heliantheae; and that it represents a connecting link between Heliantheae and Astereae. The following facts bear out such a conclusion. The bristle- or awn-like pappus, composed mostly of 2–10 (rarely to 15 according to Cabrera) slender or paleaceous bristles, is heliantheaceous and also helenieaceous rather than astereaceous. The caducous pappus is not known elsewhere in the Astereae, but there are several genera in the Heliantheae (among them *Helianthus*, *Berlandiera* in part, and *Melanthera*) which possess deciduous or even caducous pappus-bristles. Further, the resinous character of the involucre and of the leaves is shared by a number of genera in the Heliantheae and in Helenieae but is exceptional in the Astereae (being found mostly in some species of *Aplopappus*, *Chrysothamnus*, *Vanclevea*, etc.). Again, the studies by Miss Koch⁶⁵ on the ray- and disk-florets of *Grindelia squarrosa* show that the anatomy of *Grindelia* was definitely of the Heliantheae type and not at all that of the Astereae.

Finally, the receptacle in *Grindelia* shows affinities with Heliantheae rather than Astereae. In most of the species it is deeply foveolate, but close examination of the heads in anthesis shows that the foveolate appearance is due to each floret being set in a single foveola. However, each foveola is bordered on four sides by more or less coalescent outgrowths,

⁶² Cassini, H. *Diet. Sci. Nat.* 37: 468. 1825.

⁶³ Reichenbach, H. G. L. *Conspectus*. p. 107. 1828.

⁶⁴ For the complete references of the disposition of *Grindelia* by authors up to 1874, see Pfeiffer, L. *Nom. Bot.* 2: 1504. 1874.

⁶⁵ Koch, M. F. *Studies in the anatomy and morphology of the composite flower*. I. *Am. Jour. Bot.* 17: 938–952; II. 995–1010. 1930.

and each outgrowth tapers upward into an acute to subulate apex becoming several millimeters long in many species. When well developed these subulate processes strikingly resemble a reduced type of chaff. They are coriaceous, cartilaginous, or firmly membranaceous and have become conerescent, giving the appearance of a honeycombed receptacle. In *Baldwinia*, one of the Heliantheae, the chaff of the receptacle has become conerescent, coriaceous, or cartilaginous, and persistent, forming a deeply alveolate structure in which the achenes are enclosed. On account of the properties possessed in common by *Grindelia* and many Heliantheae (and also Helenieae) these foveolate outgrowths of *Grindelia* may be regarded as actually reduced or specialized chaff which has become more or less degenerate. Moreover, the dorsally pubescent terminal appendages of the stylar branches and the anthers of *Grindelia* could be included in the Heliantheae just as well as in the Astereae.

While the evidence seems to point to the actual affinity of *Grindelia* with the tribe Heliantheae, one cannot overlook the affinity of the genus with certain homochromous Astereae, such as *Vanclevea*, *Aplopappus* (especially section *Prionopsis*), *Xanthisma*, *Acamptopappus*, and perhaps *Chrysothamnus*. T. S. Brandege⁶⁶ originally placed his genus *Eastwoodia* in the Astereae on account of its involucre, style-tips, and the general habit of the desert species of *Aplopappus*, although he recognized that it differed from all other genera of the tribe by its complicate-chaffy receptacle and pappus composed of 5–8 unequal persistent awns. An astereaceous genus with a complicate-chaffy receptacle combined with a pauci-aristate pappus is certainly very anomalous; and Greene⁶⁷ recognized it as an anomalous genus of the Astereae. The genus *Eastwoodia* differs from *Grindelia* in having a persistent pappus and complicate-chaffy receptacle but it is quite closely related, much more so than are *Gutierrezia*, *Gymnosperma*, or *Penta-*

⁶⁶ Brandege, T. S. Two undescribed plants from the Coast Range. *Zoë* 4: 397–398. 1894.

⁶⁷ Greene, E. L. *Flora Franciscana*. part. IV. 361. 1897.

chaeta. According to the judgment of the present writer, *Eastwoodia* is out of place in the Astereae, and should certainly be in the Heliantheae.

Of the various homochromous astereaceous genera with which *Grindelia* in the past has been allied, attention should be directed to *Aplopappus*. In discussing its affinities with other genera, Hall⁶⁸ suggests a possible connection of the section *Prionopsis* of *Aplopappus* with *Grindelia* because the "much narrowed and deciduous pappus-awns" of the latter "closely resemble section *Prionopsis*." Later in his description of the single species, *Aplopappus ciliatus*, of the section *Prionopsis*, he says of the pappus "all bristles . . . tardily deciduous, often in groups."⁶⁹ However, the present author examined many specimens of *Aplopappus ciliatus* and found the pappus always truly persistent. With care one can actually force the pappus which is united at the base to fall off as a whole, and that is about the extent of its being deciduous. The real relationship, if any, between *Grindelia* and *Aplopappus* section *Prionopsis* is in the reduced number of pappus-bristles compared with most of the other sections. A much closer connection between *Grindelia* and *Aplopappus*, and probably the best one, is to be found in *Aplopappus occidentalis* (section *Isopappus*) which has, according to Hall,⁷⁰ a ray-pappus of 5-6 slender deciduous bristles and a disk-pappus of 1-8 deciduous bristles, and in addition possesses a viscid and glandular involucre.

Vanceleva is closely related to *Grindelia* by its resinous involucre and pappus of comparatively few (12 or so) bristles, but differs in having a persistent pappus of more numerous bristles, very elongated exerted stylar branches and appendages, leaves of entirely different insertion and position, as well as a peculiarly shedding epidermis of the stem. *Vanceleva* appears to be more closely related to *Acamptopappus* and is also related to *Chrysothamnus*. The latter in turn is

⁶⁸ Hall, H. M. The genus *Haploppaus*. Carnegie Inst. Wash. Publ. No. 389: 27. 1928.

⁶⁹ Hall, *loc. cit.* p. 84.

⁷⁰ Hall, *loc. cit.* pp. 214-216.

connected through its section *Punctati* with section *Ericameria* of *Aplopappus*.

Grindelia does not appear to be related closely to *Gutierrezia*, *Amphipappus*, and *Gymnosperma*. These genera would

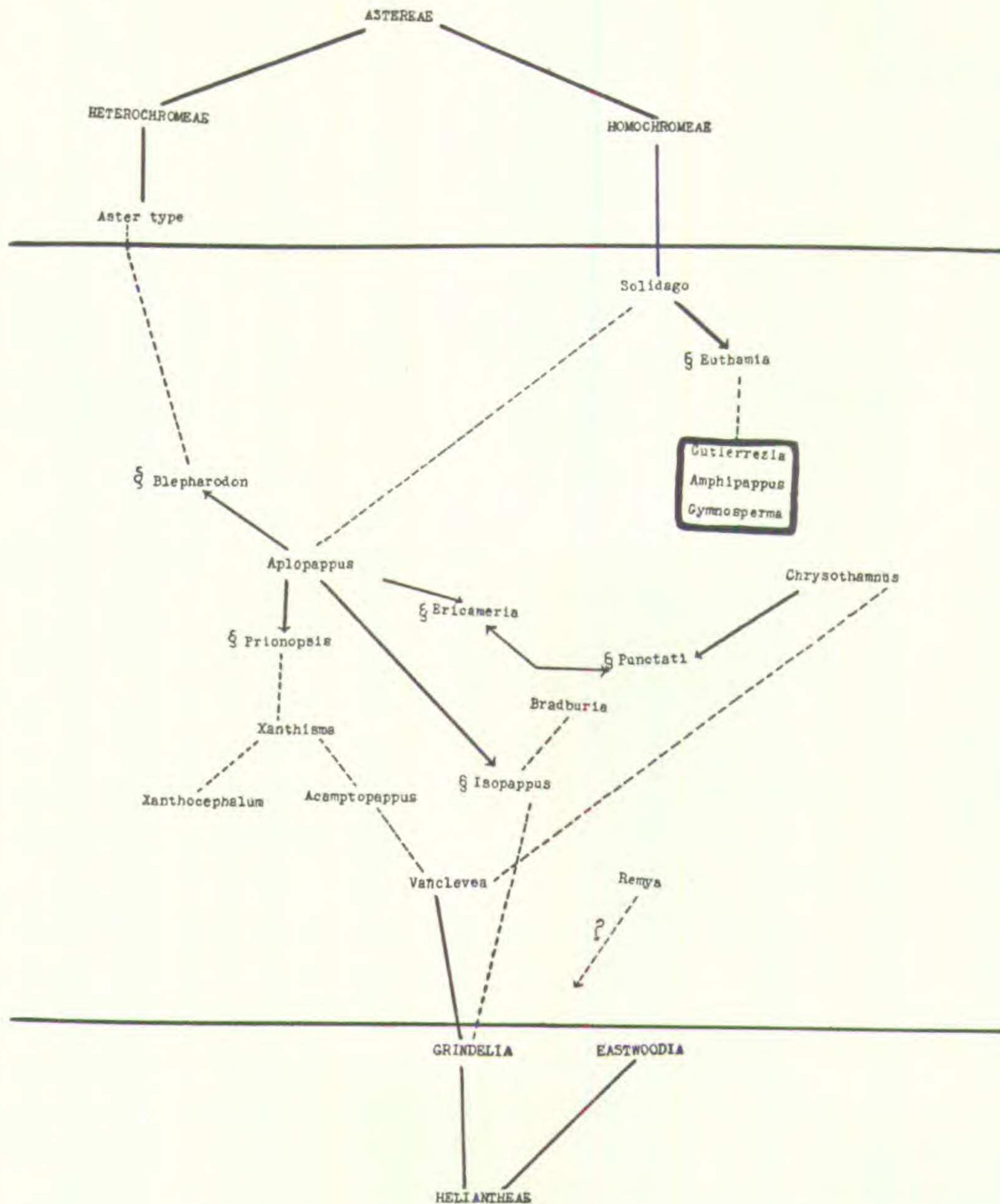


Fig. 2. Chart showing relationships of the genus *Grindelia*.

seem to be more closely allied to section *Euthamia* of *Solidago*, because of their rather numerous small heads, similar habit, and superficial similarity of involucral bracts. The pappus, however, of these genera is entirely different.

Remya, a genus of the Sandwich Islands, although usually placed near or next to *Grindelia*, is not especially closely allied, and is certainly not as near as are *Vanclevea*, *Eastwoodia*, certain species of *Aplopappus*, *Acamptopappus*, and others. *Remya* differs from *Grindelia* in having a persistent pappus, sub-bilabiate ray-corollas, small narrower heads, and in habit. Lastly, *Pentachaeta* is more closely related to other homochromous genera of the Astereae than to *Grindelia*.

It would appear that many of the homochromous Astereae are at one end of that tribe and have given rise to members which are transitional to the Heliantheae and Helenieae. *Grindelia* and *Eastwoodia* seem to be two such genera which possess characters that stamp them as being more heliantheaceous than astereaceous (fig. 2).

PHYLOGENY

Grindelia is an excellent example of a very natural genus, like *Crataegus*, *Rubus*, *Salix*, *Viola*, *Dodecatheon*, etc. Such genera, where definite homogeneity is maintained throughout and all the species exhibit the characteristic generic morphological limitations, are not likely to be confused with others. Often genera which are quite coherent allow themselves to be subdivided into natural sections or subgenera. With *Grindelia*, however, the species are so closely inter-related and give to the genus such a high degree of homogeneity that the establishment of sections would be artificial and well-nigh impossible. True, various species tend to form into little groups, but the lines are not sufficiently sharp to permit subgeneric or sectional groups. For example, the rugose surface of the mature achene in a number of Mexican species, combined with a capillary-like pappus, would be important enough for a sectional category were it not that other Mexican species with a similar type of pappus have smooth achenes. Knobby or tooth-like processes or undulate-bordered ridges at the apex of the achene are possessed by many Pacific Coast species and might be used for a sectional character, except for the fact that some Pacific Coast species possess a subtruncate apex or one with

scarcely any indication of apical processes or the like; besides there are many transitional types which it would not be possible to place in a definite category.

Rubus, *Crataegus*, *Artemisia*, *Eriogonum* have also had a relatively recent evolution or a recent cycle of rapid multiplication of types. With such genera we are having the opportunity of examining a large suite of recently evolved, closely related forms, in a conspicuously branching evolutionary tree. In most cases there are relatively so few, if any, hiatuses, that their evolutionary history is more or less apparent and requires only a careful and close analytical study to unite the relationships. Often the phylogenetic sequence is very closely correlated with the geographical distribution and limitations. In *Grindelia* this is quite evident. All the recently evolved and closely related species and varieties of the Pacific Coast and interior plains and prairies show a remarkably inter-related complex of linkages, the geographic ranges of which overlap at the margins.

Probably some of the Mexican and South American species of *Grindelia* were at one time associated with one another and were derived from a common ancestral form. They have been separated, however, since early Cenozoic time, when Central and South America were separated by seas, and they have since diverged along independent paths. Most of the North American species seem to have been derived from species of the Ozark and Edwards Plateaus and Texas Hills section. The major phylogenetic trends of the non-Mexican, North American species seem to have been closely correlated with major northward paths of migration from the Mexican species, and radiation taken place eastward and westward.

From *G. oxylepis* and its variety *eligulata* or *G. subdecurrens* of Mexico two major paths of migration are correlated with specific differentiation. *Grindelia oxylepis* has given rise to *G. arizonica* and varieties, which in turn link up with the Pacific Coast species complex and these species (*G. oxylepis* var. *eligulata* and *G. subdecurrens* of Mexico) seem to connect at several points with the species complex, *G. Havardii*-*G. squar-*

rosa-G. perennis and related types. It is possible to derive the radiate *G. Havardii* from the radiate Mexican *G. subdecurrens* because of their common characters: squarrose or spreading involueral bracts, firm resinous-punctate, evenly crenulate-serrulate leaves, and a more or less conspicuously resinous involucre. From *G. Havardii* of western Texas and adjacent New Mexico the transition to the radiate *G. squarrosa*, principally by the bracts becoming more reflexed and the pappus-awns serrulate or setulose, seems logical. By a narrowing of the leaves *G. squarrosa* var. *serrulata* has become set off from the species as the latter migrated westward into the Colorado mountain region. *Grindelia perennis* has segregated from *G. squarrosa* var. *serrulata* as the species invaded the high northern plains from North Dakota, central and northern Wyoming, and Montana northward into Canada.

Another line of derivation of *G. squarrosa* from a Mexican type is also possible. *Grindelia oxylepis* var. *eligulata*, a discoid Mexican type, has evidently given rise, on the one hand, to the eligulate *G. aphanactis* of New Mexico, Arizona, southern Colorado, and southeastern Utah, and on the other hand, to the discoid *G. squarrosa* var. *nuda* and its form *angustior*. These last two occupy a southern range from southern Kansas, western Oklahoma, and central and western Texas, the f. *angustior* being scattered in the western and northwestern portion of the Texas Panhandle region. From the discoid *G. squarrosa* var. *nuda* it is very possible that the radiate *G. squarrosa* has been derived. The latter occupies a more northern range which touches that of the discoid *G. squarrosa* var. *nuda* in northwestern Texas and southern Kansas. If *G. squarrosa* has been derived from *G. squarrosa* var. *nuda*, the only possible derivation of the latter would be from the discoid Mexican *G. oxylepis* var. *eligulata*. However, if one sought for a derivation of *G. squarrosa* through a radiate type it would have to come from *G. Havardii* and it, in turn, from the Mexican *G. subdecurrens*.

It is just as possible for a ligulate type to have evolved from a discoid one, as the reverse situation. One would suppose

that the addition of a zygomorphic, ligulate corolla to a composite head of otherwise actinomorphic flowers would denote a mark of evolutionary advance over a head with entirely actinomorphic flowers. Zygomorphy throughout the angiosperms is looked upon as an advance over actinomorphy. Hall,⁷¹ however, regarded the discoid types of *Aplopappus* as cases of suppression from ordinary radiate types, and therefore a mark of evolutionary advance. This suppression may have occurred in *G. squarrosa* var. *nuda*, but it would seem, on the basis of geographical migration northward from a Mexican ancestor, that *G. squarrosa* may well have been derived from the southern phase of *G. squarrosa* var. *nuda*, and this in turn from the Mexican *G. oxylepis* var. *eligulata*. However, the derivation of *G. squarrosa* may have been through the *G. subdecurrens*-*G. Havardii* alliance, and *G. squarrosa* var. *nuda* might be interpreted as a discoid type derived from *G. squarrosa*. *Grindelia columbiana* and *G. rubricaulis* var. *bracteosa* appear to have resulted from suppression of the ray florets of *G. nana* and *G. rubricaulis* var. *robusta* respectively.

The main line of evolution, however, concerns the Pacific Coast species. If the Mexican *G. oxylepis* is taken for the ancestral type, it is found to connect with *G. arizonica* var. *microphylla* of Arizona, and this in turn with *G. arizonica*. From *G. arizonica* two lines of development have taken place. One begins with *G. arizonica* var. *stenophylla* of southwestern Colorado and northwestern New Mexico (probably derived from *G. arizonica*), with which are allied *G. decumbens* and its variety *subincisa*, *G. laciniata*, *G. subalpina*, *G. acutifolia*, and *G. revoluta*. Related to *G. arizonica* and varieties are *G. scabra* and var. *neomexicana* of New Mexico and western Texas. Obviously related to this alliance are *G. lanceolata* and *G. texana*, both occurring on areas that have been available for plant occupation since the close of the Cretaceous (the Edwards Plateau and Texas Hills section of Texas) or even since the Paleozoic (the Ozark Plateau). From *G. lanceolata* has

⁷¹ Hall, *loc. cit.* p. 19.

been derived *G. littoralis*, a recently evolved species, occurring on the youthful, recent coastal soils about Galveston Bay.

The other line from *G. arizonica* has proceeded towards the Pacific Coast species complex. The most obvious connection is with *G. Hallii* of the Julian-Cuyamaca Lake region of San Diego County, southern California. In addition to their fairly common distributional areas, both have involucre bracts with primitive erect-appressed, or only slightly spreading, short tips, small heads, and herbaceous habit with relatively short stems. From *G. Hallii* one can derive the remaining California element. Since *G. arizonica*, the ancestor of *G. Hallii*, has in turn been derived from Mexican types similar to *G. oxylepis*, it is quite interesting to find this Sonoran element as the ancestral type from which the later California element of the genus has been derived. Moreover, the relationship of some of the Californian flora from a derived Mexican element is strongly borne out by floristic studies.⁷² A study of the northward trend of migration of *Grindelia*, with the resultant differentiation of specific and varietal types derived from *G. Hallii*, shows that two main lines of evolution have taken place: one along the coast, the other northward up the Great Valley and lower foothills of the Coast and Sierra Nevada Range. These lines have diverged in the characters of the involucre bracts, the interior valley and foothill types mostly retaining erect, ascending, spreading or squarrose involucre bracts, and the coastal line possessing a recurved or revolute type. *Grindelia Hallii* has potentialities of both types.

From the evolution of the interior type from *G. Hallii*, we find *G. procera* to be the most closely related. It has become a decidedly more luxuriant species, with larger leaves, more height, etc., but has retained the primitive small heads and relatively short involucre bracts with erect, ascending, or slightly spreading tips of *G. Hallii*. It is found in the San Gabriel Mountains of Los Angeles County and then ranges from Tulare Lake Basin in Kern and Tulare Counties north

⁷² Jepson, W. L. Man. Fl. Pl. Cal. pp. 3 and 10. 1925.

along the San Joaquin River Valley to San Francisco Bay region as far as Sacramento County. It then gives rise to *G. camporum* by enlarging the heads, lengthening the pappus awns and involucre bracts, the tips of the latter becoming elongated and conspicuously spreading or squarrose. The linkage between these two species is very evident through *G. camporum* var. *parviflora* which possesses the small heads and habit of *G. procera* but has the bracts, pappus, and achenes of *G. camporum*.

Grindelia camporum, mostly of the lower San Joaquin River Valley from Contra Costa and San Joaquin Counties south to Merced and Fresno Counties and appearing in Los Angeles County, has given rise in Los Angeles and Kern Counties to var. *australis* with recurved bracts. It is replaced by *G. camporum* var. *Davyi* along the greater part of the Sacramento River Valley and tributaries, and in the lower foothills of the western slopes of the Sierra Nevadas and of the Coast Range. In the very youthful salt marshes and estuaries of San Francisco Bay *G. camporum*, with var. *Davyi*, and *G. procera*, all of alluvial or otherwise terrestrial soils, have given rise to *G. humilis* and varieties of salt marshes. Since *G. procera* is of very recent origin and since the San Joaquin and Sacramento Rivers both represent drowned river valleys as they empty into San Francisco Bay, it would appear that *G. camporum* and its var. *Davyi*, as well as *G. procera*, have given rise at the mouths of these drowned rivers to the more youthful estuarine species. Thus, *G. camporum* or var. *Davyi* appear to have evolved in the Suisun marshes into *G. humilis* var. *paludosa*, whereas *G. humilis* and f. *reflexa* would seem to have come from either *G. procera* or *G. camporum* var. *Davyi*.

In the northern Coast Range region of California and towards the Oregon boundary, *G. camporum* var. *Davyi* develops heads with revolute or recurved bracts and shorter pappus awns, thus giving rise to *G. nana* var. *altissima* and var. *turbinella*. Cutting through the Klamath Gap (in northeastern California and southwestern Oregon) northeastwards, east of the Cascades into Oregon, northern Nevada, Washing-

ton, Idaho, and western Montana the range of *G. nana* and varieties is continued.

More or less of a continuous series from *G. Hallii* to *G. nana* and varieties has now been traced. The other line of evolution developing from *G. Hallii* is first found in *G. rubricaulis* var. *elata*. There the involucre bracts are definitely revolute or strongly recurved at the tips, a character merely beginning as a tendency in *G. Hallii*. This var. *elata* rather begins where *G. Hallii* leaves off, ranging from the boundary of southern California in San Diego County northward along the coast to Ventura County, giving rise from Orange County northward to *G. rubricaulis* var. *robusta*. On the Santa Barbara Islands and to a limited extent on the adjacent mainland in Santa Barbara County a luxuriant form, var. *latifolia*, has become differentiated from var. *robusta*. Around the Monterey Bay region, still further north, and to a limited extent on the Santa Barbara Islands, another variation, var. *platyphylla*, is to be found.

Grindelia hirsutula with varieties is found in the Coast Range hills and valleys around San Francisco Bay from Sonoma County south into San Luis Obispo County. Certain variations of it are connected through *G. hirsutula* f. *patens*, on the one hand, with *G. rubricaulis*, and on the other, with *G. camporum* var. *interioris* f. *foliacea*.

From the coastal *G. rubricaulis* var. *platyphylla* has evolved *G. arenicola*. Certain collections of these two entities occurring in the Monterey Bay Region are scarcely inseparable, perhaps due to hybridization, but northward from Carmel, Monterey County, particularly along sand dunes and coastal beaches, *G. arenicola* becomes a definite species. Approximately at its northern limit, in southern Oregon and in some places in coastal northern California, it merges into *G. stricta*, a species ranging from southern Alaska to northern California. In *G. stricta* the leaves have become much thinner, fleshier, more elongated, the basal ones not conspicuously dilated or subtruncate at apex as in *G. arenicola*, the bracts less recurved and more spreading. There are intermediates between the two which are difficult to place; these occur where the ranges of the

two species overlap. *Grindelia stricta*, in the Puget Sound and Vancouver Island region, develops an intricately interwoven series of variations, some more or less confined to particular habitats, such as sand beaches, coastal slopes, and estuaries. Some of these variations have remained more or less glabrous, while others have taken on various degrees of pubescence. In some the leaves and involucre have become more resinous, in others less so. These are all recently evolved variations which are related to the similarly geologically youthful *G. integrifolia* and var. *virgata*.

Among the Mexican species we find a similar interwoven complex, although generally the species are somewhat more distinct. The Texan *G. microcephala* and varieties have been derived through *G. tenella*, and *G. tenella*, *G. Nelsonii*, *G. grandiflora* show in turn close affinity with *G. Greenmanii*.

It is evident that various trends of evolution may have originally been initiated from one species, at least one extant species possessing morphological potentialities which would lead to several lines of development. The relatively few gaps in the development of the generic tree of *Grindelia* are due to the recent evolution of many of the species, combined most likely with the fact that many of the ancestral forms, or forms very similar to extinct ancestral forms, are extant.

The cytological work undertaken in collaboration with Dr. T. W. Whitaker⁷³ strongly corroborates the concepts of derivation and phylogeny in the present paper. The species have been found to be either diploid or tetraploid, the former being a more primitive type cytologically, morphologically, as well as geographically and geologically, whereas the tetraploid type appears to be the most recently evolved species occurring on the most youthful areas. It seems possible to trace all diploid types back to the Sonoran stock, as well as to relate all the more recently evolved tetraploid types either from other tetraploid types or from diploid stock.

⁷³ Whitaker, T. W. and Steyermark, J. A. Cytological aspects of *Grindelia* species. Bull. Torr. Bot. Club **62**: 69-73. 1935.

SPECIFIC CONCEPT

Aside from variation naturally caused by environmental factors, some of the difficulties in the differentiation of species and varieties of *Grindelia* are no doubt due to natural hybridization and probably also to other chromosomal aberrations (chiasmotypy, apogamy, etc.). Hybridization may be suspected wherever species or varieties occur in the same area and where transitional or aberrant forms are found. Variations within a species may be quite distinct within certain limited localities, but an examination of a large suite of specimens, both in the herbarium and in the field, shows that these variations comprise one long seemingly endless line. The extremes of this interwoven chain-complex may be quite distinct and remote and yet one cannot maintain them as specific entities because of the mass of transitional material. Thus, *G. rubricaulis* and var. *elata* or var. *bracteosa* are obviously distinct, and would represent definite species were it not that *G. rubricaulis* is connected with var. *platyphylla* through the pubescent var. *platyphylla* f. *pilosa*, while var. *platyphylla* is closely allied to var. *robusta* which in turn bears obvious relation to var. *elata* and var. *bracteosa*.

Many of the species have been so recently evolved that the various differentiations have not been sufficiently segregated, and a long complex of closely related series is the inevitable result. For this reason the present author has been compelled to reduce a number of species to varieties or forms or to recognize many varieties and forms. Numerous differentiations have been set off within the genus, and all such divergences from the species have been recognized. If these many tendencies and definite variations were not recognized, the inevitable "lumping" might result in too polymorphic a species. In many cases, the species, as represented by the historical type, is only an insignificant or minor part of the whole, while a variety of such a species may be the common and widely distributed type found. For instance *G. microcephala* var. *adenodonta*, *G. hirsutula* var. *brevisquama*, *G. rubricaulis* var.

robusta and var. *elata* represent the more widely dispersed and more commonly collected forms in the species, but, unfortunately are not the entities involved in the real historical nomenclatorial species.